THOMAS ANDREW KNIGHT
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THOMAS ANDREW KNIGHT IN MEMORIAM

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(WITH ONE PLATE[1] AND ONE FIGURE)

During the latter part of the eighteenth century the physiological behavior of plants challenged the attention of many investigators. The brilliant discoveries of PRIESTLY, INGEN HOUSZ, SENEBIER, and DE SAUSSURE were great historical events, and their published works form an impressive and unforgettable chapter in the history of plant physiology. To this galaxy of stellar performers must be added the name of THOMAS ANDREW KNIGHT, who, beginning his investigations during the decade from 1780 to 1790, became subsequently one of the keenest and most prolific students of plant physiology and horticulture. His publications in the *Philosophical Transactions of the Royal Society of London* began in 1795, and more than 20 papers appeared in the *Transactions* up to the year 1828. In addition he published well over 100 papers in horticulture, and several well known independent treatises. His career was brought to a close by death in 1838, at the age of 79 years.

Because he lived during a reactionary period, his work has never been fully appreciated. It seems most fitting, therefore, with the passage of a century since his death, to look back through the years with appreciation and understanding, especially understanding of the primitive state of knowledge throughout the realm of science, to appraise his work, and to commemorate his services to the science which he loved and his great practical services to mankind. His name will forever be associated with, and his work a part of, the history of biological science during the early decades of the nineteenth century.

[1] The plate has been reproduced from a photograph of an original in the private portrait collection of Dr. R. B. Harvey of the University of Minnesota. We wish to express to him our thanks and appreciation for the privilege of reproducing this fine portrait.

The first of his many contributions was entitled *Observations on the Grafting of Trees,* which was written at Elton, Herefordshire, April 13, 1795, as a letter to his friend and adviser, SIR JOSEPH BANKS, who read the letter before the Royal Society on April 30, 1795. The paper discussed the inheritance of decay among fruit trees, and the propagation of debility by grafting.

Encouraged by the reported reception of this paper, he continued, even long after he had been elected a Fellow of the Royal Society, to send his papers to Sir JOSEPH to be read. He was innately shy and modest, often apologetic for his shortcomings in "not being very deeply read in the experiments which naturalists have made on plants" and this may account for the presentation of his reports as letters to his intimate friend.

In appraising his work at the annual meeting of the Royal Society following his death, His Royal Highness the DUKE of SUSSEX, speaking as retiring president, rated the first paper published in 1795 as one of the most valuable of his contributions. This rating was based, no doubt, upon its practical aspects, because it dealt with the problem of "canker and moss," and the propagation of these diseases through grafts or layers to new trees. Plant physiologists, however, attach greater significance to his more scientific studies of gravitational and centrifugal action upon the roots and tops of plants. Many of his papers contain very valuable observations which one wishes were the possession of every student of plant physiology. Lord SUSSEX said: "Mr. Knight was a person of great activity of body and mind and of singular perseverance and energy in the pursuit of his favorite science: he was a very kind and agreeable writer, and it *would be difficult to name any other contemporary author in this or other countries who has made such important additions to our knowledge of horticulture and the economy of vegetation.*" (Italics ours.)

An examination of his papers reveals the truth of the president's estimate. The second paper, *An Account of Some Experiments on the Fecundation of Vegetables,* published in the Transactions in 1799, contains an account of some experiments on peas which he began in 1787. Interested mainly in the improvement of apples, he realized that results would be slow with perennial and slow-to-fruit varieties; he therefore decided to use annuals to obtain information more rapidly as to the effects of fertilization. Speaking of annuals he says: "Amongst these, none appeared so well calculated to answer the purpose as the common pea; not only because I could obtain many varieties of this plant of different forms, sizes, and colours; but also, because the structure of its blossoms, by preventing the ingress of insects and adventitious farina, has rendered its varieties remarkably permanent."

He records the use of the farina (pollen) of a gray pea in fertilizing a white variety. The seeds resulting from the original fertilization were not modified in appearance, but when these F_1 seeds were planted, all of the offspring produced plants with nothing but dark gray seeds. Then he says: "By introducing the farina of another white variety (or, in some instances by simple culture) I found this colour was easily discharged, and a numerous variety of new kinds produced, many of which were, in size, and in every other respect, much superior to the original white kind, and grew with excessive luxuriance, some of them attaining a height of more than twelve feet." Here we see KNIGHT observing dominance, recessive behavior, and heterosis almost 80 years before MENDEL's day. With a more complete understanding, and quantitative analysis of his results in succeeding generations, KNIGHT might easily have occupied the position in genetics now given to MENDEL. One wonders how aware MENDEL may have been of this interesting work carried on by KNIGHT nearly a century earlier; for KNIGHT had the virtue not to place his work in an obscure journal.

He turned his attention to ascent and descent of sap in trees, and showed himself a true disciple of HALES and DUHAMEL. In tracing the ascent of sap he used a deep-colored infusion of grape skins to locate the translocating tissues, and also used ringing technique for studies of sap descent in the phloem. He was always critical in his judgments, and had a fine sense of disagreement with previous authors, and with the current beliefs of his day. He says: "In the authors I have looked into, I have seen many contradictory experiments related, and many conclusions drawn from a small number of facts, and I have found much that does not well agree with the things that have come under my own observation." Speaking of leaves he says: "This organ has much engaged the attention of naturalists, particularly Mr. BONNET: but their experiments have chiefly been made on leaves severed from the trees; and, therefore, whatever conclusions have been drawn, stand on very questionable ground." His papers are full of such critical statements.

In a paper on "*Experiments and Observations on the Motion of the Sap in Trees*" read in 1804, he mentions the eleventh plate in HALES' *Vegetable Staticks* disparagingly: "The experiments and still more, the Plates of HALES, have induced naturalists to draw conclusions in direct opposition to the preceding. But the Plates of that great naturalist are not always taken correctly from nature; and Plates, under any circumstances, however fair and candid the intentions of an author may be will too often be found somewhat better calculated to support his own hypotheses, than to elucidate the facts he intends to state." KNIGHT praises DUHAMEL highly for his accuracy, overlooking the fact, apparently, that DUHAMEL copied HALES' eleventh plate for his own work published in 1758, and accepted it without question. Later KNIGHT was compelled to admit his own errors in connection with gravitational studies of sap movement in reversed stems.

The great paper on the influence of gravitation and centrifugal force on the responses of seedlings was read before the Royal Society in 1806. It bore the title: *"On the Direction of the Radicle and Germen during the Vegetation of Seeds."* The paper was not illustrated, but it is a classic of simplicity and clarity. The figure of his wheels presented in this paper is taken from Sir HUMPHREY DAVY's *Agricultural Chemistry,* published in 1813. We quote the essential paragraphs as follows: "I conceived that if gravitation were the cause of the descent of the radicle, and of the ascent of the germen, it must act either by its immediate influence on the vegetable

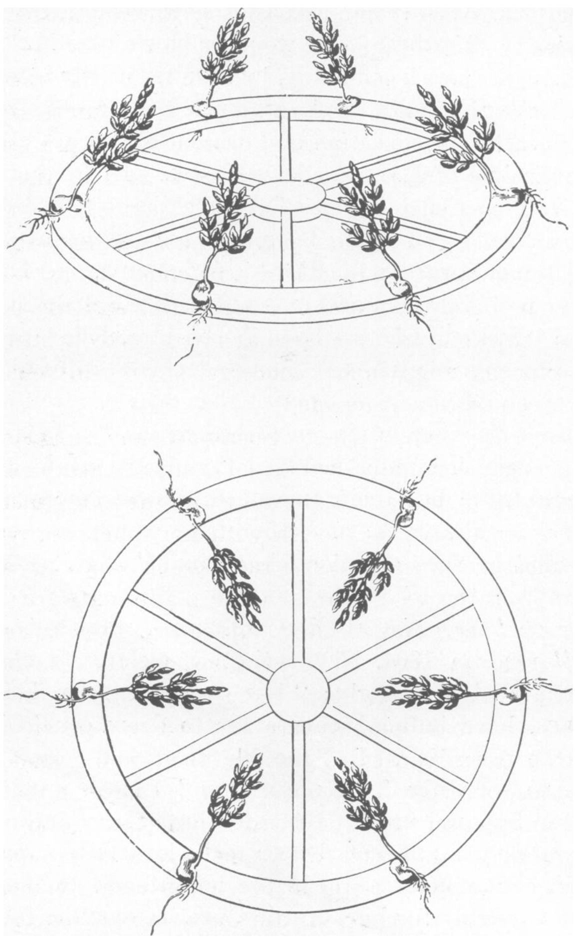

FIG. 1. Diagrammatic representation of KNIGHT's rotating wheels, showing the direction of growth. From DAVY's *Agricultural Chemistry.*

fibres and vessels during their formation, or on the motion and consequent distribution of the true sap afforded by the cotyledons: and as gravitation could produce these effects only whilst the seed remained at rest, and in the same position relative to the attraction of the earth, I imagined that its operation would become suspended by constant and rapid change of the position of the germinating seed, and that it might be counteracted by the agency of centrifugal force."

"Having a strong rill of water passing through my garden, I constructed a small wheel similar to those used for grinding corn, adapting a wheel of different construction, and formed of very slender pieces of wood, to the same axis. Round the circumference of the latter, which was eleven inches in diameter, numerous seeds of the garden bean, which had been soaked in water to produce their greatest degree of expansion were bound, at short distances from each other. The radicle of these seeds were made to point in every direction, some towards the center of the wheel, and others in the opposite direction; others as tangents to its curve, some pointing backwards, and others forwards, relative to its motion; and others pointing in opposite directions in lines parallel with the axis of the wheels. The whole was inclosed in a box, and secured by a lock, and a wire grate was placed to prevent the ingress of any body capable of impeding the motion of the wheels,. The water being then admitted, the wheels performed something more than 150 revolutions in a minute; and the position of the seeds relative to the earth was of course as often perfectly inverted, within the same period of time, by which I conceive that the influence of gravitation must have been wholly suspended."

"In a few days the seeds began to germinate, and as the truth of some of the opinions I had communicated to you, and of many others which I had long entertained, depended on the result of the experiment, I watched its progress with some anxiety, though with not much apprehension; and I had soon the pleasure to see that the radicles, in whatever direction they were protruded from the seed, turned their points outward from the circumference of the wheel, and in their subsequent growth receded nearly at right angles from its axis. The germens, on the contrary, took the opposite direction, and in a few days their points all met at the centre of the wheel. Three of these plants were suffered to remain on the wheel, and were secured to its spokes to prevent their being shaken off by its motion. The stems of these plants soon extended beyond the centre of the wheel; but the same cause, which first occasioned them to approach its axis, still operating, their points returned and met again at its centre."

"The motion of the wheel being in this experiment vertical, the radicle and germen of every seed occupied, during a minute portion of time in each revolution, precisely the same position they would have assumed had the seed vegetated at rest; and as gravitation and centrifugal force also acted in lines parallel with the vertical motion and surface of the wheel, I conceived that some slight objections might be urged against the conclusions I felt inclined to draw. I therefore added to the machinery I have described another wheel which moved horizontally over the vertical wheels; and to this, by means of multiplying wheels of different powers, I was enabled to give many different degrees of velocity. Round the circumference of the horizontal wheel, whose diameter was also eleven inches, seeds of the bean were bound as in the experiment, which I have already described, and it was then made to perform 250 revolutions in a minute. By the rapid motion of the water wheel much water was thrown upwards on the horizontal wheel, part of which supplied the seeds upon it with moisture, and the remainder was dispersed, in a light and constant shower, over the seeds in the vertical wheel, and on others placed to vegetate at rest in different parts of the box."

"Every seed on the horizontal wheel, though moving with great rapidity necessarily remained in the same position relative to the attraction of the earth; and therefore the operation of gravitation could not be suspended, though it might be counteracted, in a very considerable degree, by centrifugal force; and the difference, I had anticipated, between the effects of rapid vertical and horizontal motion soon became sufficiently obvious, The radicles pointed downwards about ten degrees below, and the germens as many degrees above, the horizontal line of the wheel's motion; centrifugal force having made both to deviate 80 degrees from the perpendicular direction each would have taken, had it vegetated at rest. Gradually diminishing the rapidity of the motion of the horizontal wheel, the radicles descended more perpendicularly, and the germens grew more upright; and when it did not perform more than 80 revolutions in a minute, the radicle pointed about 45 degrees below, and the germen as much above, the horizontal line, the one always receding from, and the other approaching to, the axis of the wheel.

"I would not, however, be understood to assert that the velocity of 250, or of 80 horizontal revolutions in a minute will always give accurately the degrees of depression and elevation of the radicle and germen which I have mentioned; for the rapidity of the motion of my wheels was sometimes diminished by the collection of fibres of conferva against the wire grate; which obstructed in some degree the passage of the water: and the machinery, having been the workmanship of myself and my gardener, cannot be supposed to have moved with all the regularity it might have done, had it been made by a professional mechanic. But I conceive myself to have fully proved that the radicles of germinating seeds are made to descend, and their germens to ascend, by some external cause, and not by any power inherent in vegetable life: and I see little reason to doubt that gravitation is the principal, if not the only agent employed, in this case, by nature."

In still others of his papers we find him solving problems that are refreshingly modern. One of them *"On the Inverted Action of the Alburnous Vessels of Trees"* contains an account of the profuse flowering even of very early varieties of potatoes, which ordinarily do not blossom, when he prevented the consumption of the carbohydrates by suppressing stolon formation. He accomplished the suppression in an ingenious fashion. Those who have given attention to the influence of clipping on forage survival and succeeding yields will appreciate this statement from a paper read in 1805: "I have constantly found, in my practice as a farmer, that the produce of my meadows has been immensely increased when the herbage of the preceding year had remained to perform its proper office till the end of the autumn, on ground which had been mowed early in the summer." And the relation of girdling to blossom-bud setting in apples receives the following comment: "It has been long known to gardeners that taking off a portion of bark round the branch of a fruit tree occasions the production of much blossom on every part of that branch in the succeeding season." If he had mentioned the high-carbohydrate content of these tissues he would truly have been a hundred years ahead of his time.

His breadth of interest is indicated by the fact that he wrote not only about many kinds of fruits and vegetables, but about insects, such as aphis and bees; and various plant diseases, such as blights, cankers, etc. He even interested himself in the formation of ice in the bottoms of rivers.

Born at Wormsley Grange, near Hereford, on August 12, 1759, son of THOMAS KNIGHT and grandson of RICHARD KNIGHT who won a fortune as an iron master, THOMAS ANDREW was educated at Ludlow School, later at Chiswick, and finally at Oxford as a matriculant in Baliol College. He was 20 years old at the time he entered Oxford. He was possessed of an inherent interest in all kinds of plants and animals and was an eager sportsman and excellent shot. He utilized these inclinations, however, only as an opportunity for studying nature. The facts and incidents collected at this early period contributed a fund of information which formed the basis of many of his subsequent investigations; and his possession of land and funds gave him every opportunity to follow his natural inclinations. After leaving Oxford he lived at Elton where all of his early papers were written. The last of his letters to Sir JOSEPH BANKS from Elton was read on February 23, 1809. The next succeeding contribution, read on June 22, 1809 was sent from Downton Castle, where THOMAS ANDREW had an estate of ten thousand acres which was deeded to him by his older brother, RICHARD PAYNE KNIGHT, who is best known as a numismatist.

While still at Elton, KNIGHT helped to found the Royal Horticultural Society in 1804 as a charter member, and became its president in 1811; this position he held for 27 years, until his death in 1838. He became a fellow of the Royal Society in 1805, was awarded the Copley medal in 1806, and was elected a Fellow of the Linnean Society in 1807. He was also awarded the first Knightian Medal of the Royal Horticultural Society, a medal that bears his portrait and which was founded and named in his honor. In addition to those mentioned above he received nine other medals and was a member of 20 Societies in various countries. All of these honors were richly deserved.

In 1791, at the age of 33, he married FRANCES FELTON whose gentleness of disposition and unceasing endeavor to promote his comfort and happiness was a major factor in his achievements. They had four children, three daughters and one son. The latter was accidently killed when near his 32nd year; this incident had a profound effect upon KNIGHT's thought and work for many years. His wife and daughters survived him at his death.

Anyone who reads THOMAS ANDREW KNIGHT's scientific contributions, his treatise *On the Manufacture of Cider and Perry* (1797), *A Treatise on the Culture of the Apple and Pear* (1797), *Pomona Herefordiensis* (1811), and his numerous practical papers on horticultural practices, must be impressed with his keen intellect, his unusual powers of observation, and his ability to express himself with force and clarity. His singular powers of memory, which he retained until his death, were of particular note. His skill in all kinds of horticultural operations, and his appreciation of the problems inherent in the production of fruits and vegetables, turned him to very practical services. One of his peculiarities was the readiness by which, with his own hands and the assistance of a common carpenter or blacksmith, he would construct all of the machinery required in his most elaborate experiments.

He placed England's horticulture on a solid foundation, and its subsequent growth and development is an enduring monument to his genius. As the years pass away, his memory will be preserved in the hearts and minds of all who are able to appreciate the time in which he lived. He stands as one of the most important contributors to our knowledge of natural history during the early part of the 19th century.

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